

A MORPHOMETRIC ANALYSIS OF VARIATION BETWEEN *ELYMUS ALASKANUS* AND *ELYMUS VIOLACEUS* (POACEAE): IMPLICATIONS FOR RECOGNITION OF TAXA

KRISTEN HARRISON¹ AND RICHARD J. HEBDA^{1,2,3}

¹ Department of Biology, University of Victoria, P.O. Box 1700, Victoria, BC, Canada V8W 2Y2
kristenh@uvic.ca

² Natural History Section, Royal BC Museum, 675 Belleville Street, Victoria, BC, Canada V8W 9W2

³ Schools of Environmental Studies and Earth Sciences, University of Victoria, P.O. Box 1700, Victoria, BC, Canada V8W 2Y2

ABSTRACT

The aim of this study was to clarify the relationships between *Elymus alaskanus* and *E. violaceus* in northwest North America. We performed a morphological and biogeographic analyses of ca. 300 widely distributed herbarium specimens. Following a univariate analysis of morphological characters used in contemporary treatments, we found no clear character, or combination of characters, that differentiates unambiguously among the taxa at the specific level. However, glume and lemma trichome length reliably separated *E. alaskanus* subsp. *hyperarcticus* from other taxa. Specimens could not be differentiated at the specific level by habitat preferences or geographic distribution as described in the most current treatments. Further, principal components analysis and cluster analysis were unable to reliably segregate specimens into groups. Discriminant analysis reliably grouped *E. violaceus* and *E. alaskanus* subsp. *hyperarcticus*, but not *E. alaskanus* specimens. In the development of a relevant treatment for *E. alaskanus* and *E. violaceus*, we recommend that (i) *E. violaceus* be treated as a subspecies of *E. alaskanus* and called *E. alaskanus* subsp. *latighunis*, and (ii) *E. alaskanus* subsp. *alaskanus* and *E. alaskanus* subsp. *hyperarcticus* continue to be recognized at the subspecific level.

Key Words: British Columbia, *Elymus alaskanus*, *Elymus violaceus*, taxonomy, *Triticeae*.

Delineation of taxa within grass tribe *Triticeae* (Poaceae) has been complicated and controversial (Dewey 1983a; Barkworth 1992; Zhang et al. 2000; Barkworth et al. 2007), with disagreement over taxonomic treatments at the generic and specific level (Hitchcock 1951; Tzvelev 1976; Löve 1980a, b; Melderis 1980; Dewey 1983b, 1984; Barkworth 1992; Stewart and Barkworth 2001; Barkworth et al. 2007). The development of a stable nomenclature for the tribe has been inhibited by the morphological complexity of the group and lack of widely accepted criteria for the most appropriate taxonomic treatment (Barkworth 1992).

Elymus L., within the *Triticeae*, has the most species and widest distribution as interpreted by Dewey (1984), Löve (1984) and Barkworth et al. (2007). It occurs worldwide in non-tropical regions and includes approximately 150 north-temperate perennial species (Dewey 1984; Zhang et al. 2000; Sun et al. 2006b; Barkworth et al. 2007). In the northwest North American province of British Columbia, Canada, there are twelve recognized species, of which *Elymus alaskanus* (Scribn. & Merr.) Á. Löve and *E. violaceus* (Hornem.) J. Feilberg are poorly resolved. *Elymus* species inhabit diverse ecological niches, including forests and forest edges, mountain

slopes and valleys, semi-deserts and grasslands (Sun et al. 2006b). *Elymus* morphology varies widely within and among species because of introgression, the ability of species to form intra- and interspecific fertile hybrids and the polyploid origin of the genus (Sun and Li 2005; Barkworth et al. 2007). Additionally, morphological variability among species is partially under environmental control (Sun and Li 2005; Sun et al. 2006a; Barkworth et al. 2007). The high levels of variability observed in morphological traits are consistent with the genetic variability observed in molecular studies (Díaz et al. 1999; Zhang et al. 2000, 2002; Sun and Salomon 2003).

Alaskan wheatgrass, *Elymus alaskanus* and Arctic wheatgrass, *Elymus violaceus* are perennial, allotetraploid species (StStHH, $2n = 4x = 28$) that illustrate the taxonomic difficulty of *Elymus* (Zhang et al. 2000; Sun and Salomon 2003; Barkworth et al. 2007). Previously, this species complex has been placed in several different taxa (cf. Hitchcock 1951; Welsh 1974; Löve 1984; Baum et al. 1991; Cody 1996; Barkworth et al. 2007) (Table 1). Morphological similarity between *Elymus alaskanus* and *Elymus violaceus* has led to contradictory taxonomic conclusions, and taxonomists are not in agreement on whether or not the two are separate species (Zhang et al.

2000; Stewart and Barkworth 2001; Sun et al. 2006a; Barkworth et al. 2007). The issue of distinguishing the two taxa morphologically is illustrated in the two comprehensive treatments covering British Columbia: *The Flora of North America* (FNA) *Volume 24* (Barkworth et al. 2007) and *The Illustrated Flora of British Columbia Volume 7* (Stewart and Barkworth 2001). Stewart and Barkworth (2001), recognize only one member at the specific level, *E. alaskanus* (Scribn. & Merr.) Á. Löve subsp. *latiglumis* (Scribn. & J.G. Sm.) Á. Löve (= *E. violaceus*), whereas Barkworth et al. (2007), recognize two species, *Elymus alaskanus* and *Elymus violaceus*. The treatment in the FNA (Barkworth et al. 2007), in accordance with Hultén (1968), asserts that *E. alaskanus* is differentiated from *E. violaceus* in having relatively shorter glumes than *E. violaceus* (Barkworth et al. 2007). Those of *E. alaskanus* are said to be $\frac{1}{3}$ to $\frac{2}{3}$ as long as the adjacent lemmas, and those of *E. violaceus* $\frac{3}{4}$ to equal to the lemma length (Barkworth et al. 2007). Following Löve (1984) and Cody (1996), Barkworth et al. (2007) further divide *E. alaskanus* into subspecies, naming plants with relatively glabrous glumes and lemmas as *E. alaskanus* subsp. *alaskanus*, and those with glumes and lemmas covered densely by trichomes as *E. alaskanus* subsp. *hyperarcticus* (Polunin) Á. Löve & D. Löve. Both taxa are mostly arctic or alpine (sometimes subalpine) species with a northern circumpolar distribution. However, the more restricted range of *E. alaskanus* is thought to distinguish it from *E. violaceus* (Barkworth et al. 2007). *Elymus alaskanus* grows across the high arctic of North America to eastern Russia, through Siberia, Alaska, northern USA and Greenland (Zhang et al. 2000; Sun and Salomon 2003), but according to the FNA distribution maps is almost absent from British Columbia (Barkworth et al. 2007: 326). The distribution of *E. violaceus* extends from Alaska across arctic Canada to Greenland and south in the Rocky Mountains to southern New Mexico (Barkworth et al. 2007). In western North America *E. alaskanus* is often associated with valleys and flat sites in low-competition habitats such as limestone outcrops, scree, moraines and dry meadows (Zhang et al. 2000; Barkworth et al. 2007), whereas *E. violaceus* favours calcareous or dolomitic rock in arctic, subalpine and alpine habitats. In general, *E. alaskanus* is thought to be found at lower elevations than *E. violaceus* (Barkworth et al. 2007).

The aim of this study is to clarify the relationships between *E. alaskanus* and *E. violaceus* by performing morphological and biogeographic analyses of herbarium specimens collected from a broad geographic range in northwest North America, and to answer two

questions. 1) Can *E. alaskanus* and *E. violaceus* be regarded as separate species in British Columbia and adjacent regions? And if so, 2) what morphological, geographical and habitat characters can be used to discriminate between the species? Our overall objective is to contribute to the development of a single taxonomic treatment for *E. alaskanus* and *E. violaceus* in northwest North America and advance our understanding of these taxa over their broader ranges. Increased knowledge of the relationship among entities will be especially useful in British Columbia because of the widespread geographic overlap of the two species and current disagreement over their treatment within the province (e.g., Stewart and Barkworth 2001; Barkworth et al. 2007).

METHODS

Nomenclatural Considerations

Two sets of infraspecific taxa can be considered in Table 1, those in the “*boreale/alaskanus*” complex and those in the “*latiglumis/violaceus/hyperarcticus*” complex. When considering the infraspecific taxa from the boreale/alaskanus column (Table 1), we regard *E. alaskanus* and *E. alaskanus* subsp. *borealis* (Turcz.) Á. Löve & D. Löve as constituting the same taxon because in general taxonomists agree that differences between the potential subspecies do not warrant recognition (Stewart and Barkworth 2001; Barkworth et al. 2007). Hultén (1968) and Welsh (1974) recognized three subspecies within *Agropyron boreale* Drob., as did Löve (1984) and Cody (1996), but they placed the subspecies in *Elymus*. Taxonomists placing the members of this nomenclatural set in *Elymus* had to change the specific epithet used from “*boreale*” to “*alaskanus*” in order to conform with the rules of the International Code of Botanical Nomenclature (McNeill et al. 2006). We followed Barkworth et al. (2007) who differed from pre-existing treatments in combining these two infraspecific taxa into a single taxon, which, according to the rules of priority, were called *Elymus alaskanus* subsp. *alaskanus*. The fundamental question concerning the treatment of “*latiglumis*” and “*violaceus*” concerns the appropriate names to be applied. Scribner and Smith (1897) originally named these plants *Agropyron violaceum* (Hornem.) Lange var. *latiglume* Scribn. & J. G. Sm. Their description provided a brief description of the new variety, but did not state how the entity differed from var. *violaceum*. Generally, taxonomists agree that “*latiglumis*” and “*violaceus*” refer to the same taxon (Stewart and Barkworth 2001; Soreng et al. 2003; Barkworth et al. 2007), with the exception of Löve (1984) who applied separate names, but this compendium of taxonomic groups within the *Triticeae* was based on

TABLE 1. HISTORICAL NOMENCLATURE OF THE *ELYMUS ALASKANUS* AND *E. VIOLACEUS* COMPLEXES IN NORTH AMERICA (MODIFIED FROM BARKWORTH 1997).

Reference	Entity			
	"boreale"	"alaskanus"	"hyperarcticus"	"latiglumis"
Turczaninow (1856)	<i>Triticum boreale</i>	—	—	—
Scribner and Smith (1897)	—	—	<i>Agropyron violaceum</i> var. <i>latiglume</i>	—
Scribner (1900)	<i>Elymus borealis</i>	—	—	—
Rydberg (1909)	—	—	<i>Agropyron latiglume</i>	—
Scribner and Merrill (1910)	—	<i>Agropyron alaskanum</i>	—	—
Drobow (1916)	<i>Agropyron boreale</i>	—	—	—
Neovski (1934)	<i>Roegneria borealis</i>	—	<i>Agropyron violaceum</i> var. <i>hyperarcticum</i>	—
Polunin (1940)	—	—	—	—
Hitchcock (1951)	—	—	<i>Roegneria borealis</i> subsp. <i>hyperarctica</i>	<i>Agropyron latiglume</i>
Beetle (1952)	—	—	—	<i>Roegneria latiglumis</i>
Löve & Löve (1956)	—	—	—	—
Polunin (1959)	<i>Agropyron boreale</i>	—	—	<i>Agropyron violaceum</i>
Hultén (1968)	<i>Agropyron boreale</i> subsp. <i>boreale</i>	<i>Agropyron boreale</i> subsp. <i>alaskanum</i>	<i>Agropyron boreale</i> subsp. <i>hyperarcticum</i>	<i>Agropyron violaceum</i> subsp. <i>violaceum</i>
Hitchcock (1969)	—	—	—	—
Hitchcock and Cronquist (1973)	—	—	—	—
Welsh (1974)	<i>Agropyron boreale</i> var. <i>boreale</i>	<i>Agropyron boreale</i> var. <i>alaskanum</i>	<i>Agropyron boreale</i> var. <i>hyperarcticum</i>	<i>Agropyron caninum</i> subsp. <i>majus</i> var. <i>latiglume</i>
Löve & Löve (1976)	<i>Elymus alaskanus</i> subsp. <i>borealis</i>	—	—	<i>Agropyron caninum</i> subsp. <i>majus</i> var. <i>latiglume</i>
Tzvelev (1976)	—	—	—	<i>Agropyron caninum</i> var. <i>latiglume</i>
Scoggan (1978)	—	—	<i>Elymus sajimensis</i> subsp. <i>hyperarcticus</i>	—
Porsild and Cody (1980)	—	—	—	<i>Agropyron trachycaulum</i> var. <i>latiglume</i>
Dore and McNeill (1980)	—	—	<i>Agropyron violaceum</i> var. <i>hyperarcticum</i>	<i>Agropyron violaceum</i> subsp. <i>violaceum</i>
Moss (1983)	—	—	—	<i>Agropyron violaceum</i>
Löve (1984)	<i>Elymus alaskanus</i> subsp. <i>borealis</i>	<i>Elymus alaskanus</i> subsp. <i>alaskanum</i>	<i>Elymus alaskanus</i> subsp. <i>hyperarcticus</i>	<i>Elymus trachycaulus</i> subsp. <i>violaceus</i>
Baum et al. (1991)	<i>Roegneria borealis</i>	—	<i>Roegneria borealis</i> or <i>R. borealis</i> var. <i>hyperarctica</i>	<i>Roegneria latiglumis</i>
Cody (1996)	<i>Elymus alaskanus</i> subsp. <i>borealis</i>	<i>Elymus alaskanus</i> subsp. <i>alaskanum</i>	<i>Elymus alaskanus</i> subsp. <i>hyperarcticus</i>	<i>Elymus trachycaulus</i> subsp. <i>violaceus</i>

TABLE I. Continued.

Reference	Entity			
	"boreale"	"alaskanus"	"hyperarcticus"	"latiglumis"
Stewart and Barkworth (2001)	—	—	—	—
Barkworth et al. (2007)	—	<i>Elymus alaskanus</i> subsp. <i>alaskanus</i>	<i>Elymus alaskanus</i> subsp. <i>hyperarcticus</i>	<i>Elymus alaskanus</i> subsp. <i>latiglumis</i>
Harrison and Hebda (this study)	—	<i>Elymus alaskanus</i> subsp. <i>alaskanus</i>	<i>Elymus alaskanus</i> subsp. <i>hyperarcticus</i>	<i>Elymus alaskanus</i> subsp. <i>latiglumis</i>

names, not the plants themselves. The name *Agropyron violaceum* var. *latiglume*, as it appears on the holotype for this entity, was called *Elymus violaceus* by Barkworth et al. (2007) in the Flora of North America not to reflect a new entity but to include *E. alaskanus* subsp. *latiglumis* [= *Agropyron latiglume* Rydb.]. Here we regard *E. violaceus* and *E. alaskanus* subsp. *latiglumis* as synonyms following the work of contemporary taxonomists (Stewart and Barkworth et al. 2001; Soreng et al. 2003; Barkworth et al. 2007).

Sampling and Measurements

Herbarium specimens from the Royal BC Museum (V), the University of British Columbia (UBC), the Canadian Museum of Nature (CAN) and the United States National Herbarium (US) were used as the basis for this study (Appendix 1). All specimens included in the analysis evidently belonged in the taxa of interest, thus none were disqualified. Potential hybrid specimens (i.e., intermediate morphologies) were not excluded from the analysis because doing so could potentially create artificial groupings. Specimens retaining historical nomenclature had current names applied to them following the Flora of North America (FNA) (Barkworth et al. 2007) and were divided into three categories (1) *E. alaskanus sensu stricto* (includes specimens named *E. alaskanus* and *E. alaskanus* subsp. *alaskanus*) (2) *E. alaskanus* subsp. *hyperarcticus* and (3) *E. violaceus*. A preliminary analysis of specimens revealed that identifiers correctly applied the name *E. a.* subsp. *hyperarcticus* to specimens with hairier glumes and lemmas as described in the FNA (Barkworth et al. 2007). Hence, we are confident that our analysis of the broader taxonomic group *E. alaskanus* did not include specimens of *E. a.* subsp. *hyperarcticus*. From herein we will refer to specimens of *E. alaskanus* and *E. alaskanus* subsp. *alaskanus* collectively as *E. alaskanus sensu stricto* (*s.s.*) and specimens including all three taxa as *E. alaskanus sensu lato* (*s.l.*). In total, 109 *E. alaskanus s.s.*, 18 *E. alaskanus* subsp. *hyperarcticus* and 169 *E. violaceus* specimens were included in the analysis. Plants originated from the northwest continental United States, Alaska and Canada (Table 2). Type specimens from CAN and US were examined separately and included (1) *Agropyron alaskanum* Scribn. and Merr. (Contrib. U.S. Natl. Herb. 13: 85. 1910. Type: United States: Alaska. Circle City. 18 Aug. 1899. *W.H. Osgood s.n.* [holotype: US]); (2) *Agropyron violaceum* var. *latiglume* Scribn. and J.G. Sm. (U. S. Dept. Agric. Div. Agrost. Bull. 4: 30. 1897. Type: United States: Montana. Gallatin Co., Lone Mountain. *Tweedy 1011* [holotype: US]); (3) *Agropyron violaceum* var. *hyperarcticum* Polunin (Bull. Natl. Mus. Canada 92 (Biol. Ser.

TABLE 2. GEOGRAPHIC ORIGIN AND NUMBER OF *ELYMUS ALASKANUS SENSU STRICTO* (N = 110), *E. ALASKANUS* SUBSP. *HYPERARCTICUS* (N = 18) AND *E. VIOLACEUS* (N = 169) SPECIMENS EXAMINED FOR MORPHOLOGICAL ANALYSIS IN THIS STUDY. AK = Alaska, AB = Alberta, BC = British Columbia, MT = Montana, NU = Nunavut, NWT = Northwest Territories, ON = Ontario, QC = Quebec, UT = Utah, WA = Washington, YT = Yukon Territory.

	AK	AB	BC	MT	NU	NWT	ON	QC	UT	WA	YT
<i>E. alaskanus</i>	9	2	38	—	—	37	—	1	—	—	23
<i>E. a. subsp. hyperarcticus</i>	7	—	—	—	1	4	—	—	—	—	6
<i>E. violaceus</i>	3	4	134	1	—	8	1	—	1	2	15

24): 95. 1940. Type: Canada: Nunavut, Baffin Is., Arctic Bay, 9 Sept. 1936. *N. Polunin 2531* [isotype: CAN].

We used 22 morphological characters for analyses (Table 3). All measurements of glume and lemma characteristics were made under 10 \times magnification to the nearest 0.1 mm using an ocular micrometer. Blade length and width, spikelet, culm, and inflorescence length were measured with a line ruler to the nearest 1mm. Spikelets were selected from the middle of the inflorescence and the glume and lemma were chosen from the same spikelet. All lemmas, regardless of their stage of development, were counted. Ratios between lower glume and spikelet length, the lower glume and lemma length, and between glume margin width at widest point to total glume length were calculated. Measurements of both glumes and lemmas did not include the awns which were considered separately.

Habitat, elevation and geographical information were recorded from herbarium sheets. All specimens from Alaska, Alberta, British Columbia, Northwest Territories, Nunavut and Yukon with sufficient geographic information on herbarium labels were mapped using ArcView 9.3 (2008).

Morphological Analysis

Univariate analysis. We used univariate analyses to examine the effectiveness of using glume to lemma ratio as the key diagnostic character separating *E. alaskanus s.l.* and *E. violaceus* (as currently done in the Flora of North America volume 24, Barkworth et al. 2007). We also considered the effectiveness of using lemma and glume trichome length to identify *E. alaskanus* subsp. *hyperarcticus*. Data did not meet assumptions for normality (Shapiro-Wilk test statistic) and homogeneity of variance (plot of residuals versus fits), thus a Kruskal-Wallis test of the equality of medians was performed as a non-parametric alternative to analysis of variance (ANOVA). Boxplots were used for visual comparison of these traits. Additionally, we took as a subset of specimens, those identified by M. Barkworth (Intermountain Herbarium, Utah State University), to analyze differences in glume

to lemma ratio among taxa while reducing the variation in the interpretation of the diagnostic criteria. This subset of data met assumptions of normality and equal variance; thus ANOVA was performed and boxplots were created to investigate differences among groups. All univariate analyses were computed with Minitab (2007). Null hypotheses were rejected at $P < 0.05$. Lower glume to lower lemma measurements and ratios of type specimens from CAN and US were examined separately.

Multivariate analysis. Multivariate analyses tests included principal components analysis, discriminant analysis and cluster analysis. Correlation matrices were constructed to investigate linear relationships between morphological variables using Pearson's product moment correlation. Lower glume length, lower lemma length and spikelet length were excluded from multivariate analyses because they were components of computed ratios and elevation was excluded because a preliminary analysis indicated it varied with latitude. Because tests require that all observations are present for all cases, we excluded anther length which had a high proportion of missing values. In total, 286 specimens were used. Morphological characters included in these analyses are reported in Table 3.

We used principal components analysis (PCA) to identify morphological characters that contributed most to the variation among specimens and to characterize the pattern of trait relationships between *E. alaskanus s.s.*, *E. alaskanus* subsp. *hyperarcticus* and *E. violaceus*. Eighteen variables were included in the analysis. PCA was performed using a correlation matrix and six principal components were computed. Factor scores were used in subsequent ANOVAs to test the significance of factors among the taxa.

To assess how well trait measures could be used to correctly classify plants into taxonomic groups, we used discriminant analysis. For this analysis a quadratic discriminant function with fits was applied. To determine if our observations could be segregated into groups that were not defined in advance we used cluster analysis. A dendrogram was produced using single linkage and Euclidean distance, with variables standard-

TABLE 3. CHARACTERS MEASURED OR RECORDED FOR ANALYSIS. *Characters used in Principal Components Analysis (PCA), discriminant analysis and cluster analysis. †Margin to glume length ratio excluded from discriminant analysis because it was highly correlated with other predictors in *E. alaskanus* subsp. *hyperarcticus*.

Character	Description
Culm	
Culm length*	Length (cm) from below the inflorescence to culm base
Blade	
Blade length*	Length (cm) of longest blade
Blade width*	Width (cm) of widest point of longest blade
Inflorescence	
Inflorescence length*	Length (cm) of longest inflorescence; without awns
Inflorescence width*	Width (mm) of widest point of longest inflorescence
Spikelet	
Spikelet length	Length (mm); awnless; spikelet from mid-inflorescence
Spikelet width*	Width (mm) at widest point; spikelet from mid-inflorescence
Glume	
Lower glume length	Length (mm) of lower glume; awnless
Lower glume width *	Width (mm) at widest point of lower glume
Glume margin width *	Width (mm) of glume margin
Glume trichome length*	Length (mm) of glume trichomes
Glume veins*	Number of glume veins
Glume awn length*	Length (mm) of glume awn
Lemma	
Lower lemma length	Length (mm) of lower lemma ; awnless
Lower lemma width*	Width (mm) of lower lemma at widest point
Lemma awn length*	Length (mm) of awn length of lower lemma
Lemma trichome length*	Length (mm) of lemma trichomes
Anther length	Length (mm) of anthers
Floret number*	Total number of florets within spikelet; all stages of development
Ratios	
Margin/glume length*†	Width of glume margin at widest point to total glume length
Glume/spikelet*	Lower glume length to spikelet length
Glume/lemma*	Lower glume length to lower lemma length
Other	
Habitat	From herbarium sheet
Location	From herbarium sheet
Elevation	From herbarium sheet

ized. All multivariate analyses were computed with Minitab (2007).

Biogeographic analysis. To determine if differences in elevation exist among *E. alaskanus* s.s., *E. alaskanus* subsp. *hyperarcticus* and *E. violaceus*, specimens were placed in latitude categories: (1) all latitudes (2) $\geq 60^\circ\text{N}$ (true arctic) (3) $55^\circ\text{--}60^\circ\text{N}$ (transition-boreal) (4) $< 55^\circ\text{N}$ (southern alpine). Data in the first three groups did not meet assumptions of normality or homogeneity of variance, thus a Kruskal-Wallis test was performed to test for differences in elevation among taxa. Data in group 4 met parametric assumptions and ANOVA was performed. For the habitat analysis, all specimens with adequate information on herbarium labels (Appendix 1) were classified into two categories (1) rocky habitats or (2) valleys/flat areas and a chi-square test was performed to look at associations between habitat type and taxa.

RESULTS

Morphological Analysis

Univariate analysis. All morphological characters generally had overlapping ranges (Table 4). Taxa differed in glume to lemma ratio (Kruskal-Wallis, $df = 2$, $P < 0.001$ adjusted for ties; Fig. 1). A subset of specimens, those identified by Barkworth, also differed in glume to lemma ratio among taxa (ANOVA, $F_{(2,113)} = 43.15$, $P < 0.001$; $R^2 = 0.423$; Fig. 2). Following ANOVA, pairwise comparisons among taxa (Tukey 95% simultaneous confidence intervals) showed no significant differences between *E. alaskanus* s.s. and *E. alaskanus* subsp. *hyperarcticus*, but did find that *E. alaskanus* subsp. *hyperarcticus* is significantly different from *E. violaceus*, and *E. alaskanus* s.s. is different from *E. violaceus*. Highly significant differences among taxa were detected for both lemma trichome length (Krus-

TABLE 4. MEAN, STANDARD DEVIATION AND RANGE (IN PARENTHESIS) FOR 22 TAXONOMIC TRAITS OF *ELYMUS ALASKANUS SENSU STRICTO*, *E. ALASKANUS* SUBSP. *HYPERARCTICUS* AND *E. VIOLACEUS*.

Variable	<i>E. alaskanus</i>	<i>E. a. subsp. hyperarcticus</i>	<i>E. violaceus</i>
Culm length (cm)	33.1 ± 1.3 (10.0–69.0)	24.26 ± 1.98 (12.0–45.1)	31.20 ± 1.17 (10.0–77.5)
Blade width (cm)	0.3 ± 0.02 (0.1–0.9)	0.3 ± 0.03 (0.1–0.5)	0.3 ± 0.01 (0.1–1.9)
Blade length (cm)	8.8 ± 0.4 (2.1–20.0)	7.4 ± 0.6 (4.2–14.0)	7.8 ± 0.4 (1.9–41.0)
Inflorescence length (cm)	7.5 ± 0.2 (3.2–15.0)	6.4 ± 0.5 (3.5–10.0)	6.9 ± 0.2 (3.1–15.0)
Inflorescence width (cm)	0.5 ± 0.02 (0.3–2.0)	0.6 ± 0.4 (0.4–1.1)	0.6 ± 0.01 (0.3–1.8)
Spikelet length (mm)	12.6 ± 0.2 (7.7–20.7)	11.4 ± 0.4 (8.8–14)	12.3 ± 0.1 (7.8–20.7)
Spikelet width (mm)	2.1 ± 0.05 (0.4–3.9)	2.2 ± 0.09 (1.8–3.1)	2.2 ± 0.03 (1.1–3.5)
Lower glume length (mm)	6.9 ± 0.2 (2.4–13.5)	5.9 ± 0.2 (5.0–7.4)	8.2 ± 0.1 (4.9–13.0)
Lower glume width (mm)	1.5 ± 0.03 (0.6–2.8)	1.4 ± 0.08 (0.7–1.9)	1.7 ± 0.02 (1.0–2.5)
Lower glume awn length (mm)	0.8 ± 0.08 (0.0–6.5)	0.7 ± 1.3 (0.2–2.6)	0.8 ± 0.04 (0.0–4.0)
Number of glume veins	2–5	2–3	2–5
Width of lower glume margin at widest point (mm)	0.4 ± 0.1 (0.0–0.8)	0.4 ± 0.02 (0.2–0.6)	0.5 ± 0.01 (0.1–1.0)
Lower lemma length (mm)	9.1 ± 0.1 (5.8–14.0)	8.7 ± 0.3 (6.9–12.0)	8.8 ± 0.08 (6.4–12.0)
Lower lemma width (mm)	1.7 ± 0.03 (0.6–2.5)	1.8 ± 0.06 (1.2–2.2)	1.7 ± 0.02 (1.0–2.5)
Lower lemma awn length (mm)	2.1 ± 0.2 (0.0–7.5)	3.3 ± 0.4 (1.0–6.2)	1.0 ± 0.08 (0.0–9.9)
Number of florets	2–6	1–4	1–6
Lower glume trichome length (mm)	0.04 ± 0.008 (0.0–0.3)	0.2 ± 0.3 (0.0–0.6)	0.007 ± 0.002 (0.0–0.3)
Lower lemma trichome length (mm)	0.2 ± 0.01 (0.0–0.6)	0.4 ± 0.02 (0.2–0.6)	0.2 ± 0.01 (0.0–1.0)
Anther length (mm)	1.2 ± 0.02 (0.7–2.1)	1.2 ± 0.05 (1.0–1.7)	1.1 ± 0.02 (0.5–1.8)
Lower glume length/ spikelet length	0.6 ± 0.01 (0.2–0.9)	0.5 ± 0.02 (0.4–0.7)	0.7 ± 0.008 (0.3–1.03)
Lower glume length/lower lemma length	0.8 ± 0.01 (0.4–1.2)	0.7 ± 0.02 (0.5–0.8)	0.9 ± 0.009 (0.7–1.5)
Glume margin width at widest point/ lower glume length	0.7 ± 0.1 (0.4–1.4)	0.7 ± 0.04 (0.3–1.0)	0.7 ± 0.01 (0.28–1.0)

kall-Wallis, $df = 2$, $P < 0.001$ adjusted for ties; Fig. 3) and glume trichome length (Kruskall-Wallis, $df = 2$, $P < 0.001$ adjusted for ties; Fig. 4). Type specimen measurements indicate that *Elymus violaceus* (= *Agropyron violaceum*

var. *latiglume*) had a glume to lemma ratio of 0.91, *Elymus alaskanus* subsp. *alaskanus* (= *Agropyron alaskanum*) had a ratio of 0.59, and *Elymus alaskanus* subsp. *hyperarcticus* (= *Agropyron violaceum* var. *hyperarcticum*) a ratio of 0.76.

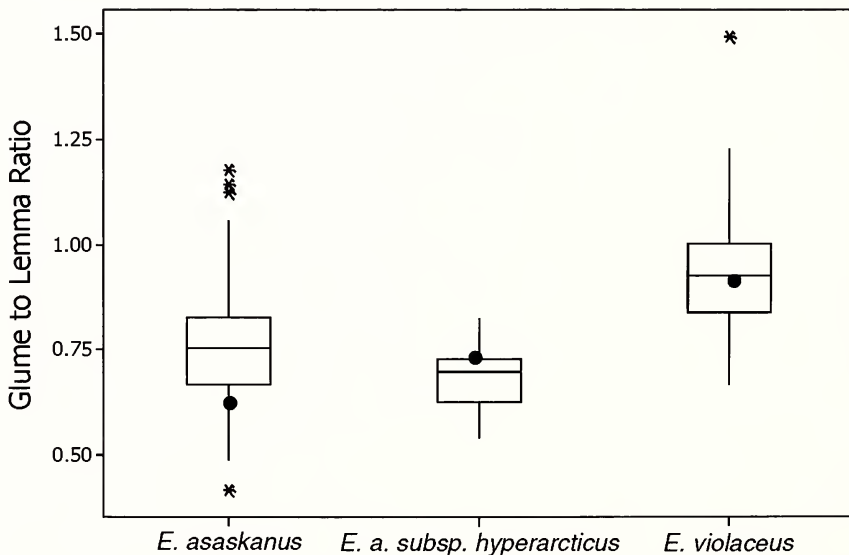


FIG. 1. Glume to lemma ratio for *Elymus alaskanus sensu stricto* ($n = 110$), *E. alaskanus* subsp. *hyperarcticus* ($n = 18$) and *E. violaceus* ($n = 169$). Glume to lemma ratio for type specimens *Elymus violaceus* (= *Agropyron violaceum* var. *latiglume*), *Elymus alaskanus* subsp. *alaskanus* (= *Agropyron alaskanum*), and *Elymus alaskanus* subsp. *hyperarcticus* (= *Agropyron violaceum* var. *hyperarcticum*) indicated by ● symbol.

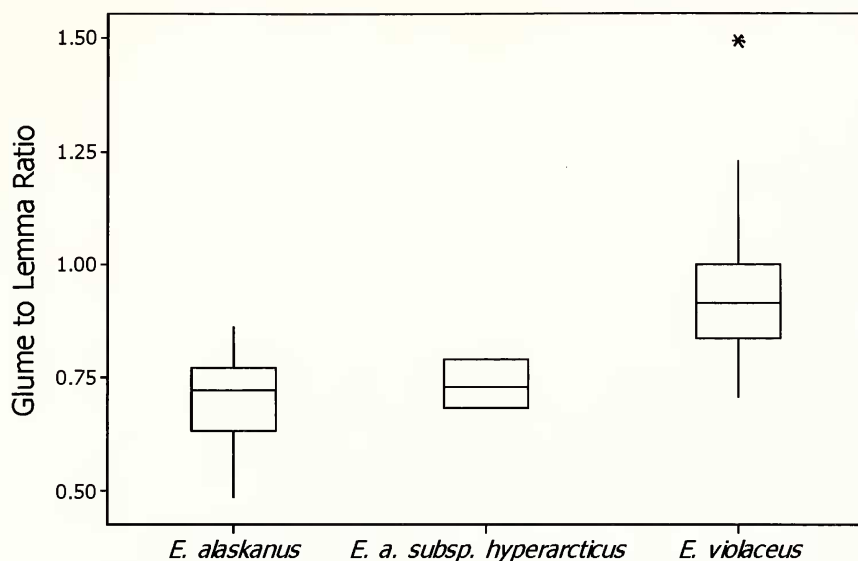


FIG. 2. Glume to lemma ratio for specimens of *Elymus alaskanus sensu stricto* ($n = 32$), *E. alaskanus* subsp. *hyperarcticus* ($n = 3$) and *E. violaceus* ($n = 81$) identified by Barkworth.

Multivariate analysis. Correlations among morphological characters used in the multivariate analysis ranged from 0.021 to 0.8, thus none were excluded from the analysis. Five principle components (PC) had eigenvalues >1 and the first three components accounted for 47% of the variation in the data set (Table 5; Fig. 5). The first principle component (PC1) accounted for 20% of the total variance, with the lower glume width and glume length to lemma length ratio and lower lemma width having the highest coefficients, and all loading positively on PC1. In contrast, blade length, lemma awn length and

culm length loaded negatively on PC1. PC2 accounted for 15.7% of the total variance and reflected increased inflorescence length, blade length and culm length, but decreased trichome lengths of both glumes and lemmas. Spikelet width, lower lemma width and glume trichome length loaded negatively on PC3 and glume to spikelet length ratio and glume trichome length loading positively.

An ANOVA using PC1 scores confirmed differences among taxa (ANOVA, $F_{(2,283)} = 28.65$, $P < 0.001$; $R^2 = 0.168$), with *E. violaceus* having significantly larger PC1 scores than either

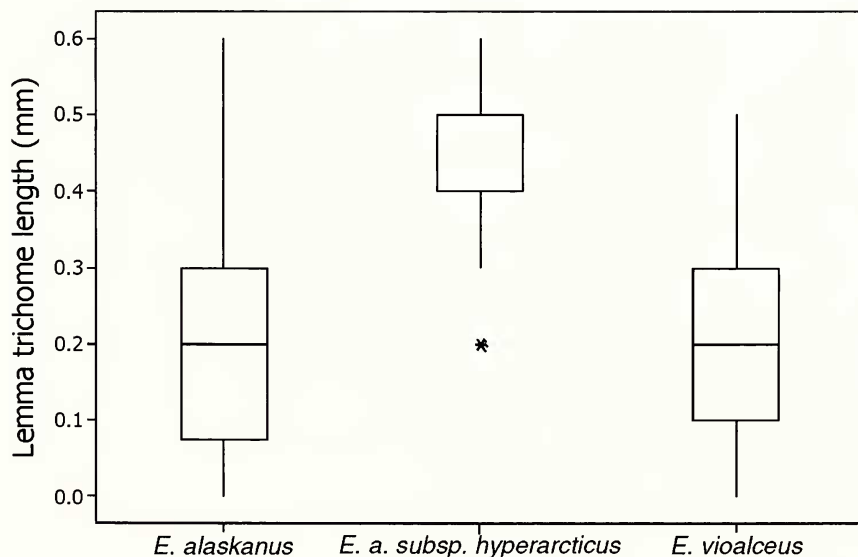


FIG. 3. Lemma trichome for *Elymus alaskanus sensu stricto* ($n = 110$), *E. alaskanus* subsp. *hyperarcticus* ($n = 18$) and *E. violaceus* ($n = 169$).

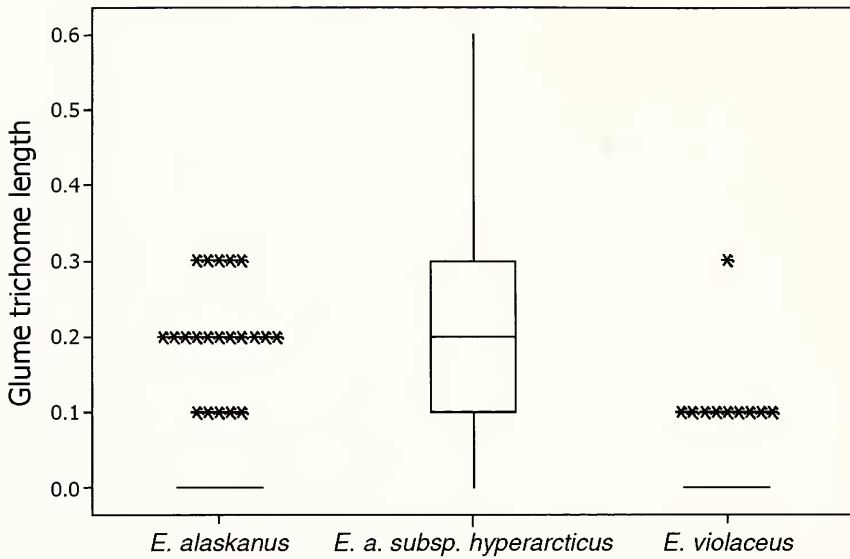


FIG. 4. Glume trichome length for *Elymus alaskanus sensu stricto* (n = 110), *E. alaskanus* subsp. *hyperarcticus* (n = 18) and *E. violaceus* (n = 169).

E. alaskanus or *E. alaskanus* subsp. *hyperarcticus* (Table 6). Pairwise comparisons among taxa of PCA factor 1 (Tukey 95% simultaneous confidence intervals) showed no significant differences between *E. alaskanus* s.s. and *E. alaskanus* subsp. *hyperarcticus*. However, *E. alaskanus* subsp. *hyperarcticus* was different from *E. violaceus*, and *E. alaskanus* s.s. was different from *E. violaceus*. ANOVA of PC2 scores showed highly significant differences among taxa (ANOVA, $F_{(2,283)} = 28.65$, $P < 0.001$; $R^2 = 0.136$), with *E. alaskanus* subsp. *hyperarcticus* different from both *E. violaceus* and *E. alaskanus* s.s. ANOVA of PC3 scores also confirmed highly significant differences among taxa (ANOVA, $F_{(2,283)} = 26.45$, $P < 0.001$; $R^2 = 0.151$). Pairwise comparisons among taxa of PC3 indicate significant differences among all taxa.

Discriminant analysis of morphological characters (Table 3) indicated that *E. alaskanus* s.s., *E. alaskanus* subsp. *hyperarcticus* and *E. violaceus* were assigned to their true group 72.1%, 100% and 93.9% of the time, respectively. When using a subset of the total morphological characters, those characters used in the FNA (Barkworth et al. 2007) including glume to lemma ratio, glume trichome length and lemma trichome length, *E. alaskanus* s.s., *E. alaskanus* subsp. *hyperarcticus* and *E. violaceus* were assigned to their true group 39.4%, 94.4% and 86.6% of the time, respectively. Cluster analysis results indicate that our observations could not be segregated into three discrete groups. All specimens fell within a single cluster.

Biogeographic analysis. Elevation differed among taxa when specimens were combined from all latitudes (Kruskall-Wallis, $df = 2$, $P < 0.001$

adjusted for ties; Fig. 6). However, significant differences for elevation between *E. alaskanus* s.l. and *E. violaceus* were not detected when specimens were grouped by latitude (1) below 55°N (Kruskall-Wallis, $df = 1$, $P < 0.090$ (adjusted for ties) (2) 55°N–60°N (Kruskall-Wallis, $df = 1$, $P < 0.0191$ (adjusted for ties) (3) above 60°N (ANOVA, $F_{(2,41)} = 0.09$, $P < 0.916$; $R^2 < 0.01$ adjusted). Note that there are no herbarium specimens of *E. alaskanus* subsp. *hyperarcticus* south of 60°N. Further, no evidence exists for association between taxa and habitat type (Fig. 7; Chi-square test $P < 0.528$). With the inclusion of recently collected specimens the distribution of the two species overlaps broadly, particularly in British Columbia (Fig. 8). This pattern differs markedly from data of Barkworth et al. (2007) where *E. alaskanus* s.l. was restricted to extreme northern BC and northward.

DISCUSSION

The close morphological association among taxa makes it difficult to differentiate among entities. We found, as Barkworth et al. (2007) did, that the glume to lemma ratio of *E. alaskanus* s.s. is significantly less than that of *E. violaceus*. Our average ratios indicate that the glumes of *E. alaskanus* s.s. and *E. alaskanus* subsp. *hyperarcticus* are on average $\frac{1}{3}$ to $\frac{2}{3}$ as long as the adjacent lemmas, and those of *E. violaceus* are $\frac{3}{4}$ to equal the lower lemma length (Fig. 1). Though the mean values for glume to lemma ratio concur with Barkworth et al. (2007), boxplots (Fig. 1) demonstrate that the range of overlap is too large for discrimination between the proposed species based on this character alone. Moreover, a subset

TABLE 5. COEFFICIENTS AND EIGENVALUES FOR THE FIRST THREE COMPONENTS OF *ELYMUS ALASKANUS SENSU STRICTO*, *E. ALASKANUS* SUBSP. *HYPERARCTICUS* AND *E. VIOLACEUS* INDIVIDUALS. * Percent of the total variability accounted for by each principle component.

Variable	PC1 (20%)*	PC2 (15.7%)*	PC3 (11.1%)*
Culm length (cm)	-0.212	0.379	0.032
Blade width (cm)	-0.094	0.308	-0.279
Blade length (cm)	-0.236	0.344	-0.158
Inflorescence length (cm)	-0.178	0.424	-0.106
Inflorescence width (cm)	0.237	0.101	-0.273
Spikelet width (cm)	0.263	0.072	-0.378
Lower glume width (cm)	0.421	0.089	0.014
Lower glume awn length (mm)	0.099	0.085	-0.129
Number of glume veins	0.084	0.278	-0.014
Width of widest point of glume margin (mm)	0.296	0.041	-0.047
Lower lemma width (mm)	0.339	0.013	-0.323
Lower lemma awn length (mm)	-0.224	0.121	-0.247
Number of florets	0.085	0.248	-0.331
Lower glume trichome length (mm)	-0.115	-0.331	-0.335
Lower lemma trichome length (mm)	0.207	-0.289	-0.212
Lower glume to spikelet length ratio	0.318	0.139	0.336
Lower glume length to lower lemma length ratio	0.346	0.210	0.284
Width of widest point of glume margin to lower lemma length ratio	0.046	-0.147	-0.146

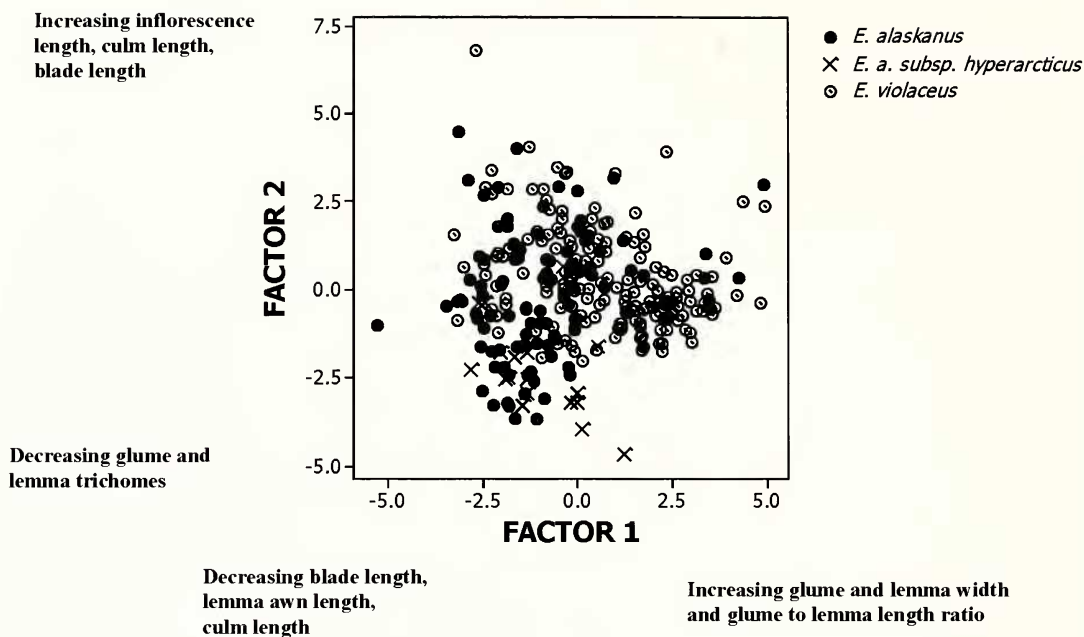
of specimens identified by Barkworth (Fig. 2) suggests that even when the distinguishing criteria are strictly applied, there is a continuum of values rather than discrete ranges for glume to lemma ratio that might indicate distinct entities. *Elymus alaskanus* subsp. *hyperarcticus* clearly has longer glume and lemma trichomes than the other taxa. *Elymus alaskanus* s.s. and *E. violaceus* trichome lengths are very similar (Figs. 3 and 4). These observations demonstrate that *E. alaskanus* subsp. *hyperarcticus* is easily distinguishable from other taxa as has been noted by others (Polunin 1940; Löve and Löve 1956; Hultén 1968; Welsh 1974; Tzvelev 1976; Löve 1984; Baum et al. 1991; Cody 1996; Barkworth 1997; Barkworth et al. 2007). Type specimens of the taxa were distinguishable based on lower glume to lower lemma ratio and followed the criteria outlined in the FNA (Barkworth et al. 2007). We expected the type specimens to fit the criteria outlined in the FNA (Barkworth et al. 2007) because they were named differently based on morphological differences of the particular specimens collected. However, it must be recognized that the usefulness of a type specimens for clarifying taxonomic issues may be limited because it represents only one population. Type specimens of *E. alaskanus* subsp. *alaskanus* (= *Agropyron alaskanum*), *E. alaskanus* subsp. *hyperarcticus* (= *Agropyron violaceum* var. *hyperarcticum*) and *Elymus violaceus* (= *Agropyron violaceum* var. *latiglume*) originated from Alaska, Nunavut and Montana, respectively and thus may be discrete compared to geographically intermediate material from British Columbia.

Using multivariate techniques we were unable to find a combination of characters that permit

an unambiguous determination of groups at the specific level. Scatterplots of PCA factors 1–3 (Fig. 5) reveal a great deal of overlap among taxa, and the most defined group appears to be *E. alaskanus* subsp. *hyperarcticus*. Correlations between PCA scores and original traits are relatively low in magnitude, thus indicating that the morphological characters represent a small proportion of the overall variability. Discriminant analysis indicated that *E. alaskanus* subsp. *hyperarcticus* and *E. violaceus* could be assigned to their predefined taxonomic groups most of the time, but that *E. alaskanus* s.s. was a less reliable grouping. Further, we did a second discriminant analysis using a subset of data (glume to lemma ratio, glume trichome length and lemma trichome length) and found that *E. alaskanus* s.s. was correctly classified only 39.4% of the time. This may indicate that people making identifications have an easier time classifying *E. violaceus* and *E. alaskanus* subsp. *hyperarcticus* specimens than they do *E. alaskanus* s.s. specimens, however why this might be remains unknown. We used cluster analysis to determine if specimens could be put into groups that were not defined in advance but the results indicate that the observations were not divisible into groups.

According to Barkworth et al. (2007) *E. alaskanus* s.l. is thought to inhabit lower elevations than *E. violaceus*. Our analysis indicates a trend for *E. violaceus* to be at higher elevations below 60°N, but these differences were not significant (Fig. 6). Above 60°N no differences were detected among taxa. Environmental conditions to which plants are exposed at similar elevations are not constant across latitudes (Pojar and MacKinnon 1994), and this may explain our

(a)



(b)

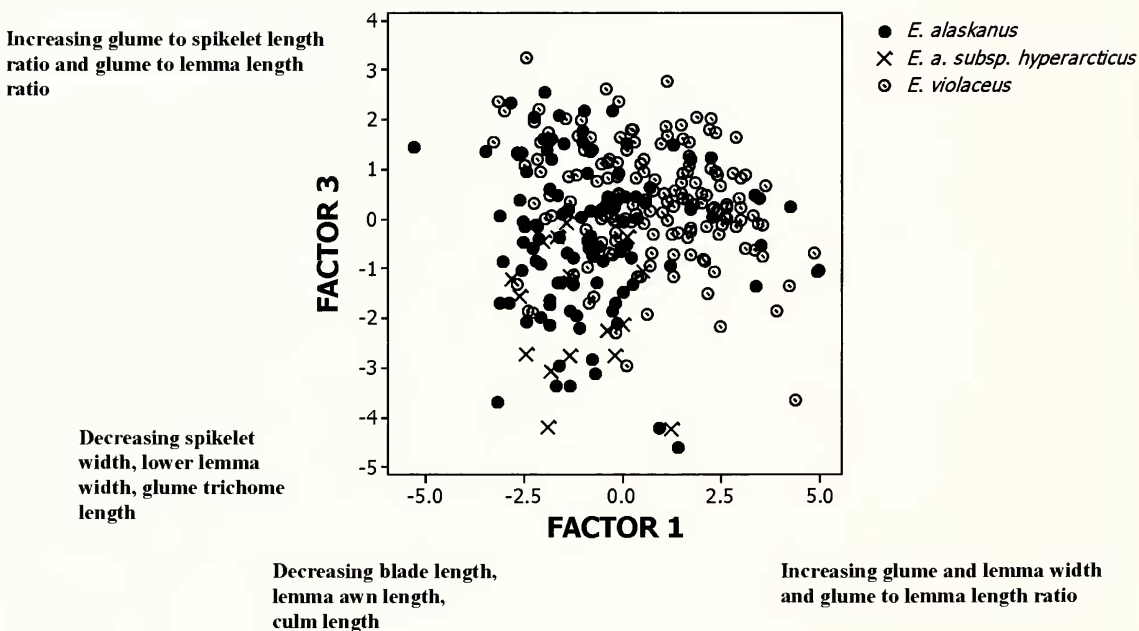


FIG. 5. Scatter graphs of principal components scores in pairwise relationships: a) factor 1 vs. factor 2; b) factor 1 vs. factor 3; c) factor 2 vs. factor 3. See Table 5 for the morphological characters included in the analysis.

(c)

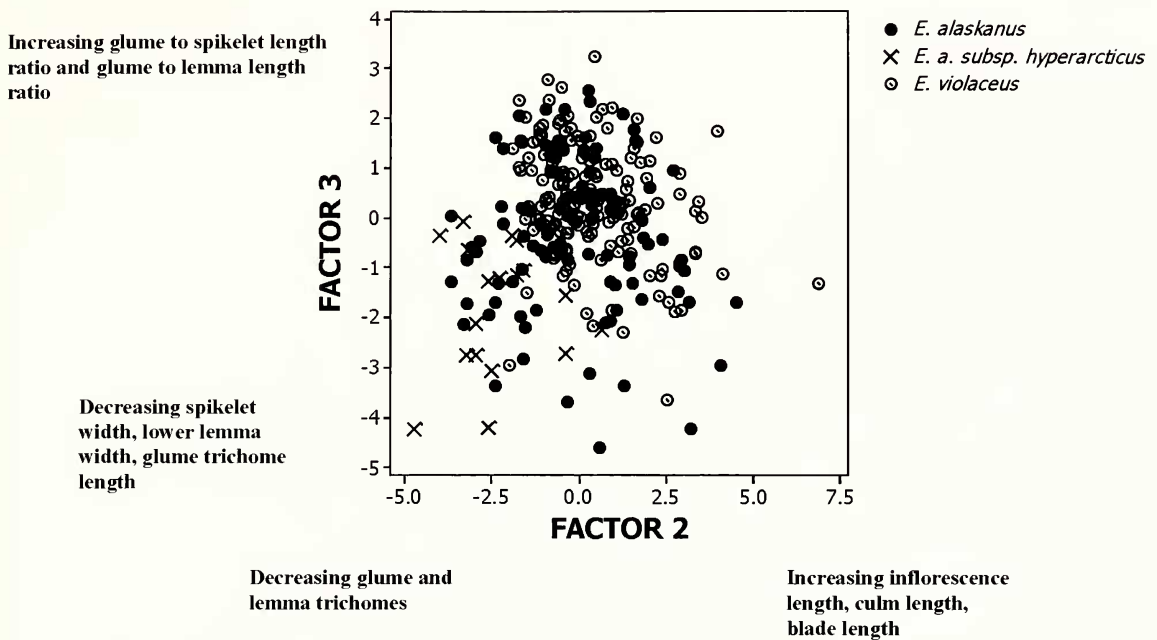


FIG. 5. Continued.

results. As a general rule, species occur at lower elevations as one moves north. At lower latitudes, plants inhabiting higher elevations are exposed to similar environmental conditions (e.g., extremes in daily temperature, shorter growing season, limited water supply, exposure to wind and colder temperatures) as plants at lower elevations but higher latitudes (Forbes 1997; Sohlberg and Bliss 1984). When latitude is not considered *E. violaceus* does appear to be found at higher elevations than *E. alaskanus s.l.* taxa which may explain the current perception that *E. violaceus* is found at higher elevation.

Contrary to Barkworth et al. (2007) who contend *E. alaskanus s.l.* is often associated with valleys/ flat areas and *E. violaceus* restricted to rocky habitats, we found that both *E. alaskanus s.l.* and *E. violaceus* were approximately equally likely to occur in either habitat type (Fig. 8). Based on our analysis, habitat cannot be used to differentiate among taxa. Habitat data recorded on herbarium sheets may be too general in order to make inferences about micro-habitat preferences. In order to analyze primary habitat difference future research should include a detailed and standardized procedure for scoring such habitat characteristics.

In the past, specimens of *E. alaskanus s.l.* have not been widely reported throughout British Columbia nor as far south as in our study (Barkworth et al. 2007). With the inclusion of new collections our map (Fig. 8) of *E. alaskanus*

s.l. and *E. violaceus* demonstrates that the distributions of the two taxa overlap broadly in range, particularly in British Columbia south of 60°N, except on the coast where no *E. alaskanus s.l.* occurs. *E. alaskanus subsp. hyperarcticus* only occurs north of 60°N. Biogeographically, the distributions of *E. alaskanus s.l.* and *E. violaceus* are of interest because it is surprising that such closely related species should both have spread and colonized similar and relatively isolated geographical areas, such as Greenland for example, since the last ice-age.

Nomenclatural Considerations

Deciding how different a taxon must be to warrant consideration as a separate entity has guided this study. In order to validate differentiating between species it is necessary to have a character or combination of characters that can discriminate unequivocally between them (Barkworth 1992). According to Barkworth et al. (2007) infraspecific taxa that show clear morphological and ecological distinctions are treated as subspecies. Despite a large sample size, wide geographic breadth and inclusion of morphological characters currently used to discriminate between *E. alaskanus s.l.* and *E. violaceus* in the Flora of North America (Barkworth et al. 2007), no clear difference morphologically, geographically or in habitat could be established in our study. According to taxonomic ranking rules

TABLE 6. ANOVA RESULTS OF PC1–3 VERSUS TAXON (*ELYMUS ALASKANUS SENSU STRICTO*, *E. ALASKANUS* SUBSP. *HYPERARCTICUS* AND *E. VIOLACEUS*). PC1 ($R^2 = 0.1625$); PC2 ($R^2 = 0.1359$); PC3 ($R^2 = 0.1516$).

	Source	DF	SS	MS	F	P
PC1	TAXON	2	172.35	86.17	28.65	<0.001
	Error	283	851.22	3.01		
	Total	285	1023.57			
PC2	TAXON	2	114.21	57.10	23.41	<0.001
	Error	283	690.32	2.44		
	Total	285	804.53			
PC3	TAXON	2	89.34	44.67	26.45	<0.001
	Error	283	477.87	1.69		
	Total	285	567.20			

following the International Code of Botanical Nomenclature a subspecies should be more similar to its parent species than different species are to one another (McNeill et al. 2006). Yet, the most distinct entity in the group studied here was *E. alaskanus* subsp. *hyperarcticus*. In fact Barkworth (1997), after examining specimens of *E. alaskanus* subsp. *hyperarcticus*, suggests that the entity is so distinct that it should not be included in the same species as *E. alaskanus* subsp. *alaskanus* and recommended it be group within *E. sajanensis* (Nevski) Tzvelev as Tzvelev (1976) had done (Fig. 1). If morphological differences between *E. alaskanus* s.s. and *E. alaskanus* subsp. *hyperarcticus* warrant subspecies designation than how could less variation between *E. alaskanus* s.s. and *E. violaceus* warrant species designation?

Preparing morphological identification keys when the characters holding a group together are non-morphological is not practical. Based on this study, there is no meaningful method to separate North American *E. alaskanus* s.s. and *E. violaceus* either morphologically or geographically. Thus, we propose a nomenclatural reconsideration of the *E. alaskanus* s.s. and *E. violaceus* complex based on the specimens used in this study and suggest that *Elymus alaskanus* is most correctly applied to all specimens that we examined following the International Code of Botanical Nomenclature (McNeill et al. 2006). Concurrent with the treatments of Löve (1984), Cody (1996) and Barkworth et al. (2007), *E. alaskanus* subsp. *hyperarcticus* should continue to be treated as a subspecies of *E. alaskanus*. Sub-specific recognition is warranted for *E. alaskanus* subsp. *hyperarcticus* based on glume and lemma trichome length. With respect to this feature, Barkworth et al. (2007) consider the trichomes of *E. alaskanus* subsp. *alaskanus* up to 0.2mm long and *E. alaskanus* subsp. *hyperarcticus* trichomes 0.2–0.5mm long. We observed that some trichomes of *E. alaskanus* subsp. *alaskanus* could reach 0.3mm rather than 0.2mm and some trichomes of *E. alaskanus* subsp. *hyperarcticus* could reach 0.6mm. Also, glume trichomes

exceeded the glume margins in every specimen of *E. alaskanus* subsp. *hyperarcticus*. In the future, an analysis in which trichome density is quantitatively assessed may be useful.

We recommend the name *E. alaskanus* subsp. *alaskanus* continue to be used for those specimens with glabrous glumes or glumes covered sparsely by trichomes following Barkworth et al. (2007). Unlike the treatment in the Flora of North America (Barkworth et al. 2007), we believe *E. violaceus* should not be regarded as a separate species from *E. alaskanus* for those specimens with relatively long glumes. If recognized at all, it should be considered a subspecies of *E. alaskanus*. At the sub-specific level, the epithet “*latiglumis*” has priority following Article 11.4 of the International Code of Botanical Nomenclature (McNeill et al. 2006). The most appropriate name for those entities with relatively long glumes is *E. alaskanus* subsp. *latiglumis* rather than *E. violaceus* which would be the name that takes priority at the specific level. It would be practical to follow the treatment of Barkworth et al. (2007) and call specimens with glumes 1/3–2/3 as long as the adjacent lemmas *E. alaskanus* subsp. *alaskanus* or *E. alaskanus* subsp. *hyperarcticus* (depending on trichome length) and specimens with glumes 3/4 as long as, to slightly longer than the adjacent lemmas, *E. alaskanus* subsp. *latiglumis*. Based on our observations, there is no evidence for a third taxon in the complex, namely *E. violaceus*, within the region of our study. Having not compared *E. violaceus* specimens used in this study to Scandinavian and Greenlandic specimens we cannot comment on whether or not they are similar entities to those found in British Columbia. For a thorough taxonomic revision of the complex, field and population studies over the whole circumboreal distribution must be made. Common garden experiments would be useful to examine specific morphological character differences as well.

This study illustrates the challenges to taxonomists of creating effective dichotomous keys that reflect biological reality. We attempted to differentiate between *E. alaskanus* and *E. viola-*

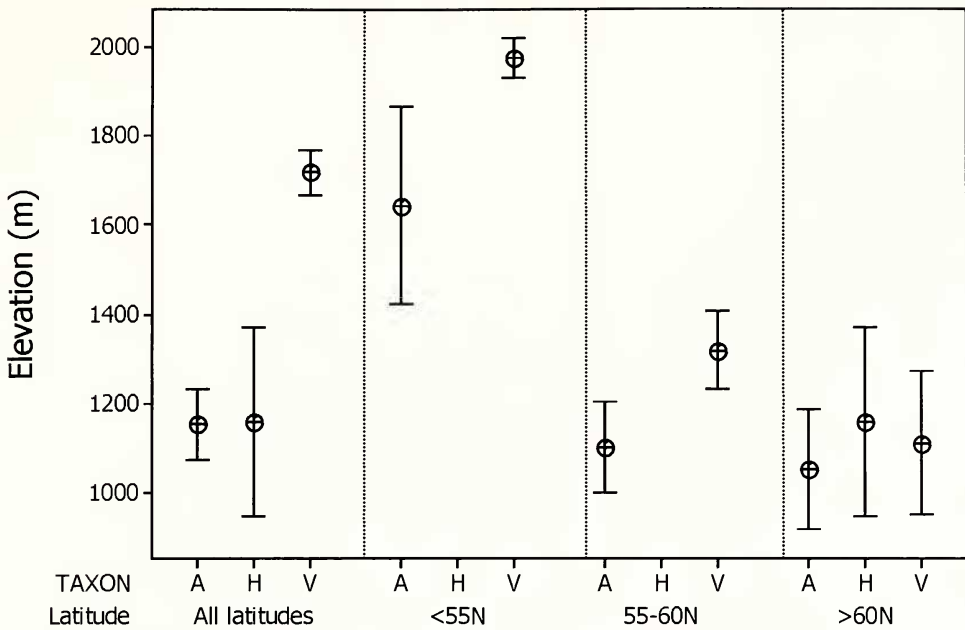


FIG. 6. Mean elevation (m) of taxa for 4 categories of latitude: (1) all latitudes (A: $n = 54$, H: $n = 7$, V: $n = 128$); (2) $<55^{\circ}\text{N}$ (A: $n = 7$, V: $n = 83$); (3) 55°N – 60°N (A: $n = 26$, V: $n = 29$); (4) $>60^{\circ}\text{N}$ (A: $n = 21$, H: $n = 7$, V: $n = 16$). Bars are one standard error from the mean. *E. alaskanus* (A); *E. alaskanus* subsp. *hyperarcticus* (H); *E. violaceus* (V).

ceus using published diagnostic features but were unable to do so using morphological characters, habitat preferences, or geographic distribution. We determined that the range of overlap of significant morphological characters examined of

E. alaskanus and *E. violaceus* was too great to discriminate between taxa. We also found that *E. violaceus* and *E. alaskanus* inhabit similar habitats and have overlapping geographic ranges and elevations. Our analysis indicates that *E. alaska-*

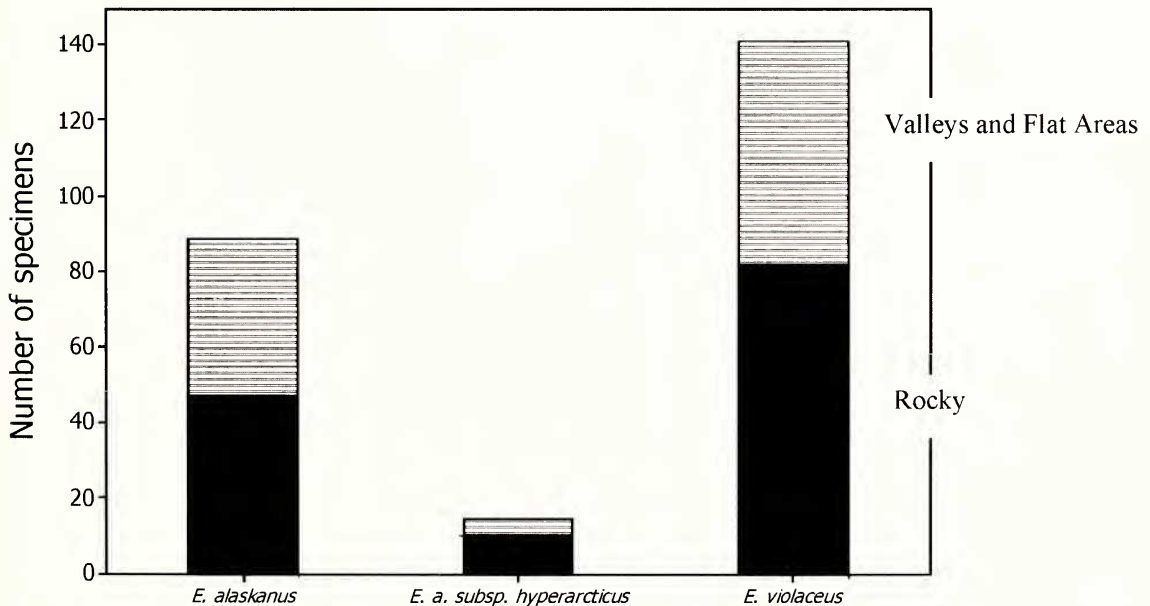


FIG. 7. A mosaic plot for habitat type and taxa. The stripped bars represent the number of specimens found in valleys and flat areas and the black bars represent the number of specimens found in rocky habitats. *E. alaskanus sensu stricto* $n = 89$; *E. alaskanus* subsp. *hyperarcticus* $n = 15$; *E. violaceus* $n = 141$.

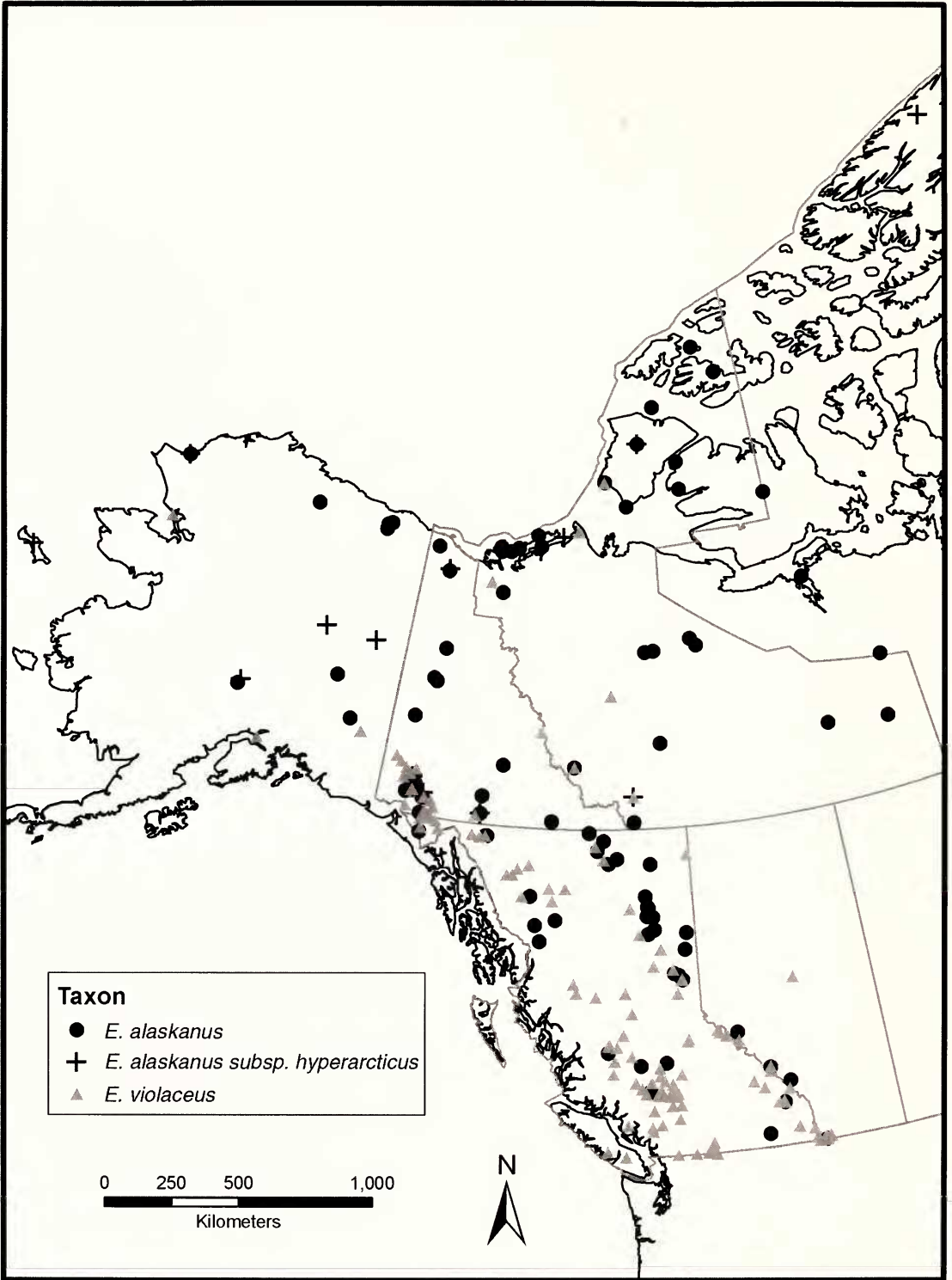


FIG. 8. Geographic distribution of *Elymus alaskanus sensu stricto*, *E. alaskanus* subsp. *hyperarcticus* and *E. violaceus* specimens from Alaska, Alberta, British Columbia, Northwest Territories, and Yukon used in this study.

mus and *E. violaceus* are potentially the same species with three infraspecific subspecies including *E. alaskanus* subsp. *alaskanus*, *E. alaskanus* subsp. *latiglumis* and *E. alaskanus* subsp. *hyperarcticus*. New geographic distribution records of specimens, particularly in British Columbia, should be included in future maps of the species ranges. For future analysis we recommend a similar analysis of other closely related species such as *E. scribneri* (Vasey) M.E. Jones and *E. trachycaulus* (Link) Gould with which *E. violaceus* has been known to form intermediates and *E. macrourus* (Turcz.) Tzvelev of which large specimens of *E. alaskanus* resemble (Barkworth et al. 2007). Further morphological analysis in combination with genetic studies including the European and eastern North American part of range may help clarify relationships between taxa. Knowledge concerning genetic relationships among these taxa is still incomplete, but the accumulation of information suggests a close genetic relationship between *E. alaskanus* and *E. violaceus*, thus supporting our findings (Zhang et al. 2000, 2002; Sun and Salomon 2003; Sun et al. 2006). Using morphological types based on spike and vegetative characters, Zhang et al. (2000) investigated genetic variation and structure among *Elymus alaskanus* populations from a broad geographical area and found that allozyme patterns revealed clear similarities among types of “tall *hyperarcticus*”, “*hyperarcticus*”, “*latiglumis*”, “*virescens*”, and “*violaceus*”. The taxon “*violaceus*” was found to be more similar to “*hyperarcticus*” and “*latiglumis*” than to “*virescens*” (Zhang et al. 2000). Zhang et al. (2002) and Sun and Salomon (2003) report that morphological types “*violaceus*” and “*latiglumis*” are genetically more similar to each other than to “*hyperarcticus*”, though later Sun et al. (2006) found a close genetic relationship between *E. alaskanus* subsp. *hyperarcticus* and *E. violaceus*. Future genetic studies should clarify how differentiation among morphological types was made, particularly between “*violaceus*” and “*latiglumis*” types given that these are currently regarded as synonyms (Stewart and Barkworth et al. 2001; Soreng et al. 2003; Barkworth et al. 2007). Studies which correlate morphology with genetic variability may help clarify the relationships between taxa.

ACKNOWLEDGMENTS

We would like to thank Geraldine Allen, Mary Barkworth, Adolf Ceska, Valerie Huff, Ken Marr and David Mazzucchi who offered many helpful suggestions to improve this paper. A special thank you to Jean Richardson and Zoë Lindo for editing the manuscript and help with the statistical analysis. Thank you to Brad Vidal for his assistance in mapping. We also thank the curators of the CAN, UBC, and US herbaria for the loan of specimens and John Pinder-Moss for his assistance in the herbarium at the Royal BC Museum (V).

LITERATURE CITED

- ARCVIEW 9.3. © Copyright 2008. ESRI. 380 New York St. Redlands, CA.
- BARKWORTH, M. E. 1992. Taxonomy of the *Triticeae*: a historical perspective. *Hereditas* 116:1–14.
- . 1997. *Elymus alaskanus*. Nomenclature set. Website <http://herbarium.usu.edu/openherbarium/elymalnm.html> [accessed 11 April 2011].
- , J. J. N. CAMPBELL, AND B. SALOMON. 2007. *Elymus*. Pp. 289–326 in *Flora of North America* Editorial Committee (eds.), *Flora of North America North of Mexico*, Vol. 24. New York, NY.
- BAUM, B. R., C. YEN, AND J. L. YANG. 1991. *Roegneria*: its generic limits and justification for its recognition. *Canadian Journal of Botany* 69:282–294.
- BEETLE, A. A. 1952. New names for Wyoming wheatgrasses. *Rhodora* 54:195–196.
- CODY, W. J. 1996. *Flora of the Yukon Territory*. NRC Research Press, Ottawa, ON.
- DEWEY, D. R. 1983a. Historical and current taxonomic perspectives of *Agropyron*, *Elymus*, and related genera. *Crop Science* 23:637–642.
- . 1983b. New nomenclatural combinations in the North American perennial *Triticeae* (Gramineae). *Brittonia* 35:30–33.
- . 1984. The genomic system of classification as a guide to intergeneric hybridization in the perennial *Triticeae*. Pp. 209–279 in J. P. Gustafson (ed.), *Gene manipulation in plant improvement*. Plenum Publishing Corporation, New York, NY.
- DÍAZ, O., B. SALOMON, AND R. VON BOTHMER. 1999. Genetic variation and differentiation in Nordic populations of *Elymus alaskanus* (Scrib. ex Merr.) Löve (Poaceae). *Theoretical and Applied Genetics* 99:210–217.
- DORE, W. G. AND J. MCNEILL. 1980. *Grasses of Ontario*. Monograph 26, Research Branch. Agriculture Canada. Ottawa, ON.
- DROBOW, V. P. 1916. *Trudy Moskovskogo Instituta Narodnogo Khozyaistva* 16:84.
- FORBES, B. C. 1997. Tundra disturbance studies. IV. Species establishment on anthropogenic primary surfaces, Yamal Region, northwest Siberia, Russia. *Polar Geography* 21:79–100.
- HITCHCOCK, A. S. 1951. *Manual of the grasses of the United States*. Miscellaneous Publications No. 200. U.S. Department of Agriculture, Washington, DC.
- 2nd ed. revised by A. Chase. 1971. Dover Publications, Inc., New York, NY.
- . 1969. Gramineae. Pp. 384–725 in C. L. Hitchcock, A. Cronquist, M. Ownbey, and J. W. Thompson (eds.), *Vascular plants of the Pacific Northwest, Part I*. University of Washington Press, Seattle, WA.
- AND A. CRONQUIST. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA.
- HULTÉN, E. 1968. *Flora of Alaska and neighboring territories*. Stanford University Press, Palo Alto, CA.
- LÖVE, A. 1980a. IOPB chromosome number reports LXVI. Poaceae-*Triticeae*-Americanae. *Taxon* 29: 166–169.
- . 1980b. Chromosome number reports LXVII. Poaceae-*Triticeae*. *Taxon* 29:350–351.

- . 1984. Conspectus of the *Triticeae*. Feddes Repertorium 95:425–521.
- AND D. LÖVE. 1956. Cytotaxonomical conspectus of the Icelandic flora. Acta Horti Gothoburgensis 20:188.
- AND ———. 1976. Nomenclatural notes on Arctic plants. Botaniska Notiser 128:497–523.
- MCNEILL, J., F. R. BARRIE, H. M. BURDET, V. DEMOULIN, D. L. HAWKSWORTH, K. MARHOLD, D. H. NICOLSON, J. PRADO, P. C. SILVA, J. E. SKOG, J. H. WIERSEMA, AND N. J. TURLAND (eds. and compilers). 2006. International code of botanical nomenclature (Vienna Code) adopted by the Seventeenth International Botanical Congress, Vienna, Austria, July 2005. Website <http://ibot.sav.sk/icbn/main.htm> [accessed March 2009].
- MELDERIS, A. 1980. *Elymus*. Pp. 192–198 in T. G. Tutin, V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb (eds.), *Flora Europaea*, Vol. 5. Cambridge University Press, Cambridge, UK.
- MINITAB INC. 2007. Version 15.1.30.0. Minitab Inc., State College, PA.
- MOSS, E. H. 1983. *Flora of Alberta*, 2nd ed., revised, J. G. Packer. University of Toronto Press, Toronto, ON.
- NEVSKI, S. A. 1934. Tribe *Hordeae* Benth. Pp. 264 in V. L. Komarov (ed.), *Flora of the U.S.S.R.*, Vol. 2, Leningrad, USSR.
- POLUNIN, N. 1980. Botany of the Canadian eastern Arctic. Part 1 Pteridophyta and Spermatophyta. National Museum of Canada, Bulletin No. 92. Canada Department of Mines and Resources, Ottawa, ON.
- . 1959. Circumpolar Arctic flora. Clarendon Press, Oxford, UK.
- PORSILD, A. E. AND W. J. CODY. 1980. Vascular plants of continental NWT, Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, ON.
- POJAR, J. AND A. MACKINNON. 1994. *Plants of the Pacific Northwest coast revised: Washington, Oregon, British Columbia and Alaska*. B.C. Ministry of Forests and Lone Pine Publishing, Vancouver, BC.
- RYDBERG, P. A. 1909. *Distichlis dentata* sp. nov. Bulletin of the Torrey Botanical Club 36:539.
- SCOGGAN, H. J. 1978. The Flora of Canada: Part 2. National Museum of Natural Sciences, Ottawa, ON.
- SCRIBNER, F. L. 1900. American grasses—III (illustrated). Descriptions of the tribes and genera. Bulletin 20. United States Department of Agriculture, Division of Agrostology, Washington, DC.
- AND E. D. MERRILL. 1910. The grasses of Alaska. Contributions from the United States National Herbarium 13:47–92.
- AND J. G. SMITH. 1897. Native and introduced species of the genera *Hordeum* and *Agropyron*. United States Department of Agriculture, Division of Agrostology, Report of the Agrostologist 4:28.
- SOHLBERG, E. H. AND L. C. BLISS. 1984. Microscale pattern of vascular plant distribution in two high arctic plant communities. Canadian Journal of Botany 62:2033–2042.
- SORENG, R. J., G. DAVIDSE, P. M. PETERSON, F. O. ZULOAGA, E. J. JUDZIEWICZ, T. S. FILGUEIRAS, AND O. MORRONE. 2003. Catalogue of new world grasses (Poaceae): IV. Subfamily Pooideae. Contributions from the United States National Herbarium 48:1–730.
- STEWART, H. AND M. BARKWORTH. 2001. *Elymus*. Pp. 132–135 in G. W. Douglas, D. V. Meidinger, and J. Pojar (eds.), *Illustrated flora of British Columbia*, Vol. 7: Monocotyledons (Orchidaceae through Zosteraceae). B.C. Ministry of Sustainable Resource Management and B.C. Ministry of Forests, Victoria, BC.
- SUN, G. AND W. LI. 2005. Molecular diversity of species of the *Elymus trachycaulus* complex and their relationships to non-North American taxa. *Plant Systematics & Evolution* 256:179–191.
- AND B. SALOMON. 2003. Microsatellite variability and heterozygote deficiency in the arctic-alpine Alaskan wheatgrass (*Elymus alaskanus*) complex. *Genome* 46:729–737.
- , J. SHEE, AND B. SALOMON. 2006a. Molecular diversity and relationships among *Elymus trachycaulus*, *E. subsecundus*, *E. virescens*, *E. violaceus*, and *E. hyperarcticus* (Poaceae: *Triticeae*) as determined by amplified fragment length polymorphism. *Genome* 49:1160–1169.
- , H. TANG, AND B. SALOMON. 2006b. Molecular diversity and relationships of North American *Elymus trachycaulus* and the Eurasian *E. caninus* species. *Genetica* 127:55–64.
- TURCZANINOW, N. S. 1856. *Flora baicalensi-dahurica*, Vol. 2. Moscou University Publication, Moscow, USSR.
- TZVELEV, N. N. 1976. Tribe 3. *Triticeae* Dumort. Pp. 147–181 in A. A. Fedorov (ed.), *Poaceae URSS*. Nauka Publishing House, Leningrad, USSR.
- WELSH, S. L. 1974. *Anderson's flora of Alaska and adjacent parts of Canada*. Brigham Young University Press, Provo, UT.
- ZHANG, X. O., B. SALOMON, R. VON BOTHMER, AND O. DIAZ. 2000. Patterns and levels of genetic differentiation in North American populations of the Alaskan wheatgrass complex. *Hereditas* 133:123–132.
- , ———, AND ———. 2002. Application of random amplified polymorphic DNA markers to evaluate intraspecific genetic variation in the *Elymus alaskanus* complex (Poaceae). *Genetic Resources and Crop Evolution* 49:397–407.

APPENDIX I

SPECIMENS EXAMINED

* = Accessions included in mapping analysis. ° = Accessions included in habitat analysis. Herbarium abbreviations: V = Royal BC Museum; CAN = Canadian Museum of Nature; UBC = University of British Columbia; US = United States National Herbarium.

Elymus alaskanus (Scribn. & Merr.) Á. Löve—CANADA. ALBERTA. UBC: 62034*°, 82554*. BRITISH COLUMBIA. V: 61973*, 76995*°, 105917*°, 106136*°, 125951*, 16671*, 17803*, 24489*, 79126*°, 91608*°, 194719*°, 195414*°, 195468*°, 196196*°, 196201*°, 196244*°, 196245*°, 196433*°, 198508*°, 198528*°, 198554*°, 198634*°, 198638*°, 198656*°, 198740*°, 198752*°, 198759*°, 198762*°, 198879*°.

198883*^o, 198895*^o, 198926*^o, 198931*^o, 198961*^o,
 199623*, 199783*^o; **UBC**: 169655*^o, 42328*^o. NORTH-
 WEST TERRITORIES. **CAN**: 127440*^o, 127441*^o,
 127442*^o, 127443*^o, 127444*, 200030*^o, 203081*^o,
 203082*^o, 203084*^o, 268362*^o, 270867*, 279113*,
 279114A*^o, 279322*^o, 39283*^o, 39286*^o, 39288*,
 39329*, 527868*^o, 529498*, 530883*^o, 530891*^o,
 582469*^o, 584015*^o, 585091*^o, 585093*^o; **UBC**:
 111282*^o, 113135*^o, 113185*, 171348*^o, 171489*^o,
 171504*^o, 171572*^o, 36871*, 37095*^o, 90155*^o;
 V25042*^o. QUEBEC. **V**: 114219. YUKON. **CAN**:
 276347*^o, 276351*^o, 276598*^o, 303292*^o, 306804*^o,
 318450*, 39772*^o, 454931*^o, 53085*^o, 549414D*^o; **UBC**:
 119413*^o, 181579^o, 27873*^o, 99014*^o, 99023*^o, 99743*^o;
V: 118217*^o, 118228*^o, 122789*, 137591*^o, 137592*,
 137610*^o, 137611*^o. USA. ALASKA. **CAN**: 211188*^o,
 211190*^o, 211191*^o, 248032*^o, 274084*^o, 211188*^o,
 211190*^o, 211191*^o, 248032*^o, 274084*^o, 276349*^o,
 367095*^o, 514133^o, 514134*^o; **US**: 592341 holotype.

Elymus alaskanus subsp. *hyperarcticus* (Polunin) Á.
 Löve & D. Löve—CANADA. NORTHWEST TERRI-
 TORIES. **CAN**: 203083*, 203085*^o, 225486^o,
 279114B*^o. NUNAVUT. **UBC**: 184460*^o; **US**: 203113
 isotype. YUKON. **CAN**: 260928*^o, 270276*^o, 454932*^o;
UBC: 99024*^o, 115538*^o; **V**: 198867*^o. USA. ALASKA.
CAN: 225257*^o, 270277*^o, 274083*^o, 318764*^o,
 366745*^o, 367096*^o; **V**: 37905*.

Elymus violaceus (Hornem.) J. Feilberg—CANADA.
 ALBERTA. **CAN**: 514030*^o; **UBC**: 21928*^o, 77875*^o; **V**:
 25062*^o. BRITISH COLUMBIA. **UBC**: 145869*^o,
 145871*^o, 145872*^o, 155889*^o, 155890*^o, 156195*^o,
 17254*, 17375*, 17410*^o, 17413*, 17429*, 21923*^o,

21925*^o, 220654*^o, 45622*^o, 58312*, 60491*^o, 67864*^o,
 86401*^o, 86433*^o, 98384*^o, 988386*^o; **V**: 123194,
 104896*^o, 106180*^o, 106188*^o, 107666*^o, 112825*^o,
 11309*^o, 115058*^o, 118641*^o, 118669*^o, 118989*^o,
 119525*^o, 119606*^o, 119616*^o, 119758*^o, 119767*^o,
 120201*^o, 120270*^o, 120310*^o, 127184*^o, 127185*,
 127186*^o, 127187*, 131360*^o, 132206*^o, 137599*,
 13699*, 137663*^o, 141176*^o, 141179*^o, 147702*,
 147703*, 147705*^o, 148290*^o, 160614*^o, 160623*,
 163871*, 16741*, 170331*^o, 17763*, 184000*,
 188109*^o, 18826*, 189980*^o, 189981*^o, 191286*,
 191307*^o, 191896*^o, 196248*, 199824*, 200057*,
 200534*^o, 200900*^o, 200910*^o, 200979*^o, 201806*,
 23978*^o, 25520*^o, 27856*^o, 27867*^o, 30232*^o, 31833*,
 32552*^o, 36900*^o, 36919*^o, 36929*^o, 36943*, 404*,
 44524*^o, 44565*^o, 48251*^o, 58714*^o, 59089*^o, 61972*,
 69404*^o, 71451*^o, 71457*^o, 75509*^o, 76343*^o, 76927*^o,
 7695*, 79578*^o, 80869*^o, 83134*^o, 83135*^o, 83137*,
 83139*^o, 83171*^o, 83172*^o, 83780*^o, 87478*^o, 87478*,
 87482*^o, 88408*^o, 88434*^o, 88444*^o, 91014*^o, 91060*^o,
 91279*^o, 91346*^o, 91374*^o, 91562*^o, 91576*^o, 91865*^o,
 91878*^o, 92000*^o, 92641*, 93241*^o, 96089*^o, 96733*,
 HR08020*, 117436*^o. NORTHWEST TERRITO-
 RIES. **CAN**: 39289*, **UBC**: 182645*, 18398*, 83427*,
 90154*^o, 96157*^o; **V**: 141141*^o, 141142*^o. ONTARIO.
UBC: 17437. USA. ALASKA. **CAN**: 514025*^o,
 514027*^o, 514028*^o. MONTANA. **V**: 44690; **US**:
 556692 holotype. UTAH. **V**: 141282^o. WASHING-
 TON. **V**: 96357^o, 137603^o. YUKON. **UBC**: 99022*^o,
 99658*^o; **V**: 137595*^o, 137604*^o, 137605*, 137607*,
 137608*^o, 137609*^o, 137612*^o, 137613*^o, 87601*^o,
 87657*^o, 87738*^o, 87857*^o, 98891*^o.